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Palynological Study of *Cheilanthes* and *Astrolepis* (Pteridaceae) Species from Northwestern Argentina

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ABSTRACT.—The spore morphology of *Cheilanthes* and *Astrolepis* species from northwestern Argentina was analyzed using light microscopy and scanning electron microscopy. Three patterns of sporoderm structure were found: two exclusive and different structures in *A. sinuata* and the *C. squamosa* group, and a typically cheilanthoid structure with diverse sculptures in the rest of the species of *Cheilanthes*, i.e., *C. bonariensis*, *C. buchtienii*, *C.* cf. *cucullans*, *C. obducta*, and *C. volcanensis*. Sporophytic features such as hairs with "tongue and groove" wall cells and dixylic vascular strands are also mentioned in *C. obducta*. Similar spore characteristics are correlated with sporophyte morphology in some of the recognized groups. Spore-size differences, abnormalities in spore type, abortion and number of spores per sporangium (16, 32) suggest polyploidy and/or apogamy in some specimens of *C. buchtienii*, *C. obducta*, and *C. squamosa*, and in all samples of *A. sinuata* and *C. bonariensis*.

The present paper is the second in a series of studies on cheilanthoid ferns preliminary to an ongoing project, "Atlas of Spores of Pteridophyta of Northwestern Argentina" (Morbelli, in prep.). Perispore structure and stratification offer some interesting substructures and variations. Previous papers (Ranker, 1989; Tryon and Lugardon, 1991) have shown that detailed analysis of the exospore and perispore can provide valuable information in cheilanthoid ferns. The aim of these papers is to characterize each species of the region from the palynological point of view and to assess whether spore morphology is useful in the systematics of the group. When necessary, sporophytic features are included for comparative analysis of species groups.

METHODS

In the first part of this study (Morbelli and Michelena, 1989), the following species of *Cheilanthes* were treated: *C. marginata* Kunth, *C. micropteris* Sw., *C. myriophylla* Desv., *C. notholaenoides* (Desv.) Weath., *C. pilosa* Goldm., *C. poeppigiana* Mett. ex Kuhn, and *C. pruinata* Kaulf. The present paper includes the species previously recognized as part of *Notholaena* (Tryon, 1956; de la Sota, 1977) and later placed into *Cheilanthes* (Tryon and Tryon, 1982) and *Astrolepis* (Benham and Windham, 1992). The following taxa were analyzed: *A. sinuata* (Lag. ex Sw.) D.M. Benham & Windham, *C. arequipensis* (Maxon) R.M. Tryon & A.F. Tryon, *C. bonariensis* (Willd.) Proctor, *C. buchtienii* (Ro-

senst.) R.M. Tryon, *C.* cf. *cucullans* Fée (de la Sota and Ponce, 1992), *C. obducta* Mett. ex Kuhn, *C. squamosa* Hook. & Grev. and *C. volcanensis* de la Sota.

Samples of spores and observations of sporophytes were taken from herbarium specimens (LIL,LP,SI). Spores were treated with 3% hot sodium carbonate for 2 min in order to preserve the perispore before acetolysis (Erdtman 1960). Spores were mounted in glycerine-jelly on glass slides; cover slips were sealed with parafin. Slides are accessioned in the Palynology Area, Botany Department of the Facultad de Ciencias Naturales y Museo de La Plata. Olympus BH2 and BHB microscopes were used for the light microscopy (LM) analysis.

For scanning electron microscopy (SEM), the material was treated with hot sodium carbonate (3%) for 2 min, washed in distilled water, and suspended in ethanol (96%), prior to mounting on stubs and examination using a JEOL JSM-35 CF instrument. Wall fractures for studying ultrastructure with SEM were made with ultrasonic equipment. Then the material was transferred through capillary tubes to acetate plates, to which spores adhered. Later the material was sputter-coated with gold.

Measures of the number of spores per sporangium were obtained by placing a single, mature sporangium in a drop of water-glycerine (50%) medium, and heating gently to crush the sporangium. The large-sized spores were measured and cited separately.

For descriptions of spore morphology, the terms proposed by Tryon and Tryon (1973) and Morbelli and Michelena (1989) were used. The classification of Tryon and Tryon (1982) was adopted for recognition of species groups.

Results

In the following descriptions, spore dimensions and sizes of structures are given as the range followed by the mean in parentheses, except where variation was negligible. The abbreviations De and Dp refer to the spore diameters in equatorial and polar views, respectively.

1. **Astrolepis sinuata** (Lag. ex Sw.) D.M. Benham & Windham.—*Cheilanthes sinuata* (Lag. ex Sw.) Domin.—Fig. 4E–H.

Description.—Spores: trilete, with triangular outline in polar view, straight sides and rounded corners; De 53.0–98.0 (79.0) μm, Dp 78.3–85.5 (82.8) μm. Laesura arms: 24.3–38.7 (32.7) μm long and 2.7 μm high, straight, tenuimarginate. Exospore: yellow, 1.1–4.6 (2.5) μm thick, rugulate, 2-layered. Perispore: pale brown to yellow, 0.7–1.3 (0.8) μm thick, 1-layered; folded. Folds short, 0.9–4 (2.7) μm high; conic with rounded apex in section; densely distributed, resulting in a rugulate surface. Folds sometimes radially oriented at the proximal pole and concentrically distributed at the distal one. Background sculpture: mixed (granules, baculae, gemmae, and echinae) sparsely and randomly distributed, 1.3-1.6 (1.4) μm high.

Comments.—In all of the material studied, ripened spores were found, but

TABLE 1. Spore numbers per sporangium and spores sizes for various spore types in the specimens of *Astrolepis sinuata* examined in the present study. Spore sizes are listed as ranges, followed by means in parentheses.

Specimen number	Types of spores and sizes (μm)				Number of spores per sporangium
	Trilete	Monolet	Inter-mediate	Alete	
Castillón s.n. (LIL)	53–96 (71)	74.4–93.6 (84)	76.8	—	32
Budin 11818 (LIL)	62–96 (82)	—	—	125–127 (126)	32
Lillo 3860bis (LIL)	65–98 (84)	84	106	110.4	32; 16

abnormalities, such as double, monolete, intermediate, and alete spores also were found within the same samples. The spores per sporangium were 32 and in 1 specimen were 32 and 16 (see Table 1). Larger sizes in spore diameters than those given by Benham (1995: 120) were estimated in all the specimens of the study area.

SPECIMENS EXAMINED.—Jujuy, Maimará, Hualchin, *Budin 11828* (LIL); Tucumán, Rosario de la Frontera, *Lillo 3860bis* (LIL); Trancas, Las Higueritas, *Legname & Cuezzo 4632c* (LIL); Catamarca, Ambato, El Potrero, Quebrada de Los Nacimientos, *Castillón* s.n. (LIL 16998).

2. **Cheilanthes arequipensis** (Maxon) R.M. Tryon & A.F. Tryon.—Fig. 1A–C.

DESCRIPTION.—Spores: trilete, with triangular outline straight sides and round corners in polar view. De 48.6–56.7 (51.7) μm; Dp 45.0–51.3 (47.9) μm. Laesura arms: straight, 20.7–36.0 (27.7) μm long, crassimarginate with ends frequently bifurcate. Exospore: yellowish to brown, 2.2–2.7 (2.5) μm thick, 2-layered, verrucate. Verrucae 1.3–1.8 (1.6) μm high, 3.6–4.9 (4.4) μm in diam.; smaller at the proximal pole (2.8–4.3 (3.6) μm in diam). Some verrucae fused at the distal pole. Perispore: hyaline, 0.4–0.8 (0.6) μm thick, strongly attached to the exospore, 1-layered, granular.

COMMENTS.—Monolete spores were found in *Cristóbal & Türpe 13* (LIL) with two kinds of exospore sculpture: smooth and verrucate. The verrucae are small.

SPECIMENS EXAMINED.—Jujuy, Tilcara, Cerro Negro, *Cristóbal & Türpe 13* (LIL); Mina Aguilar, *Broucher* s.n. (LIL 333888).

3. **Cheilanthes bonariensis** (Willd.) Proctor.—Fig. 2A–C.

DESCRIPTION.—Spores: trilete, with circular to subcircular outline in polar view. De (a) 63.9–80.1 (70.4) μm; De (b) 69.7–80.1 (72.7) μm; Dp 67.5 μm. Laesura arms: straight, 30.6–39.6 (33) μm long, 3.6 μm high, 1.7 μm thick, reaching the equator, crassimarginate. Exospore: brown, 1.5–3.1 (2.2) μm thick, 2-layered, smooth. Perispore: pale yellow to yellow, 1.8–4.5 (2.8) μm thick, strongly attached to exospore, 3-layered; inner layer thin; middle layer well developed, thick, composed of threads fused in several levels; outer layer thick, with undulate margin; closed structure (Morbelli and Michelena, 1989),

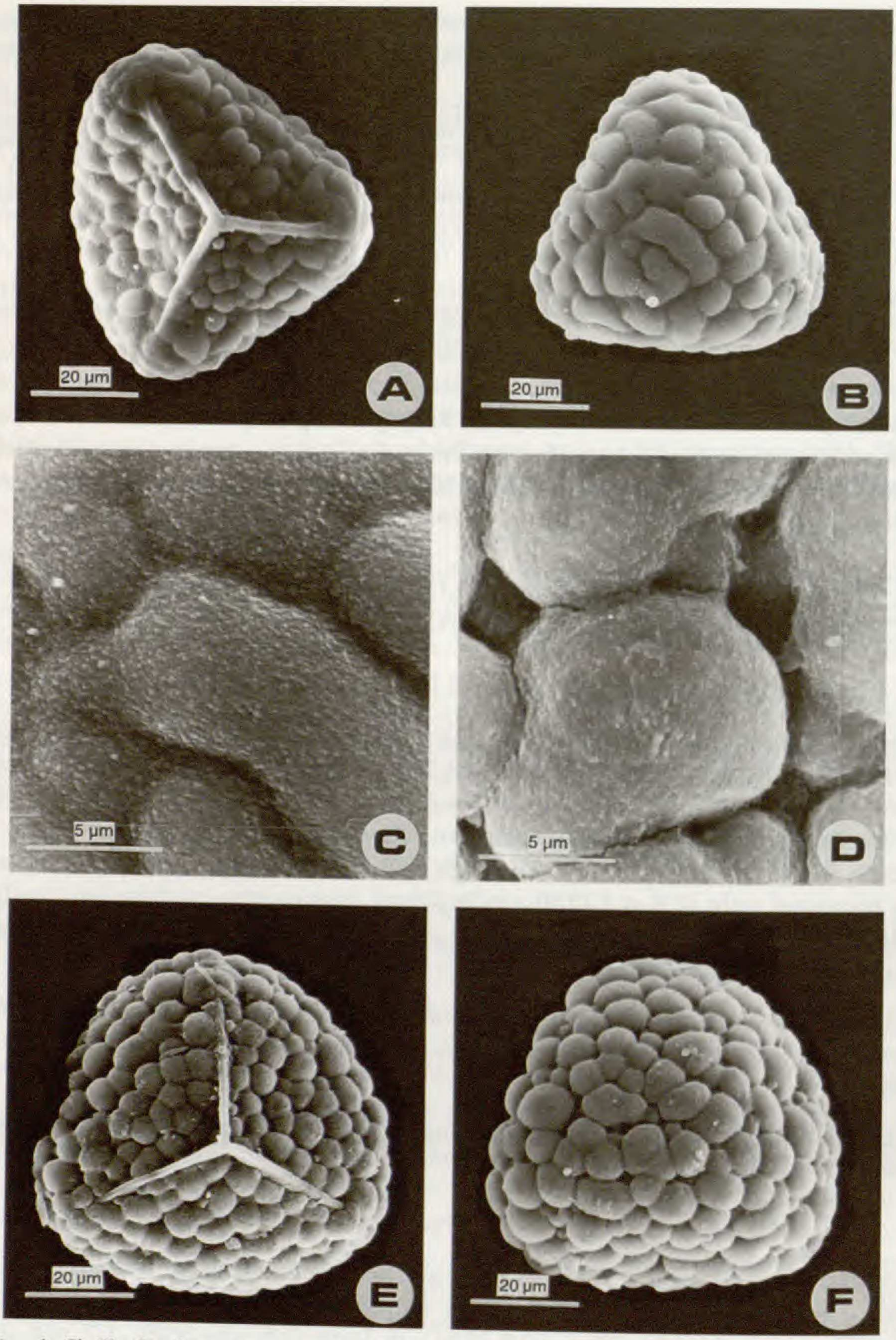

FIG. 1. A–C) *Cheilanthes arequipensis*. A) Proximal view. B) Distal view. C) Surface detail, showing the verrucate exospore and the granulate perispore on it (*Cristóbal & Türpe 13*, LIL). D–F) *Cheilanthes squamosa*. D) Surface detail, showing round verrucae of the exospore and the scabrate perispore on it. E) Proximal view. F) Distal view (*Sleumer & Vervoorst 2526*, LIL).

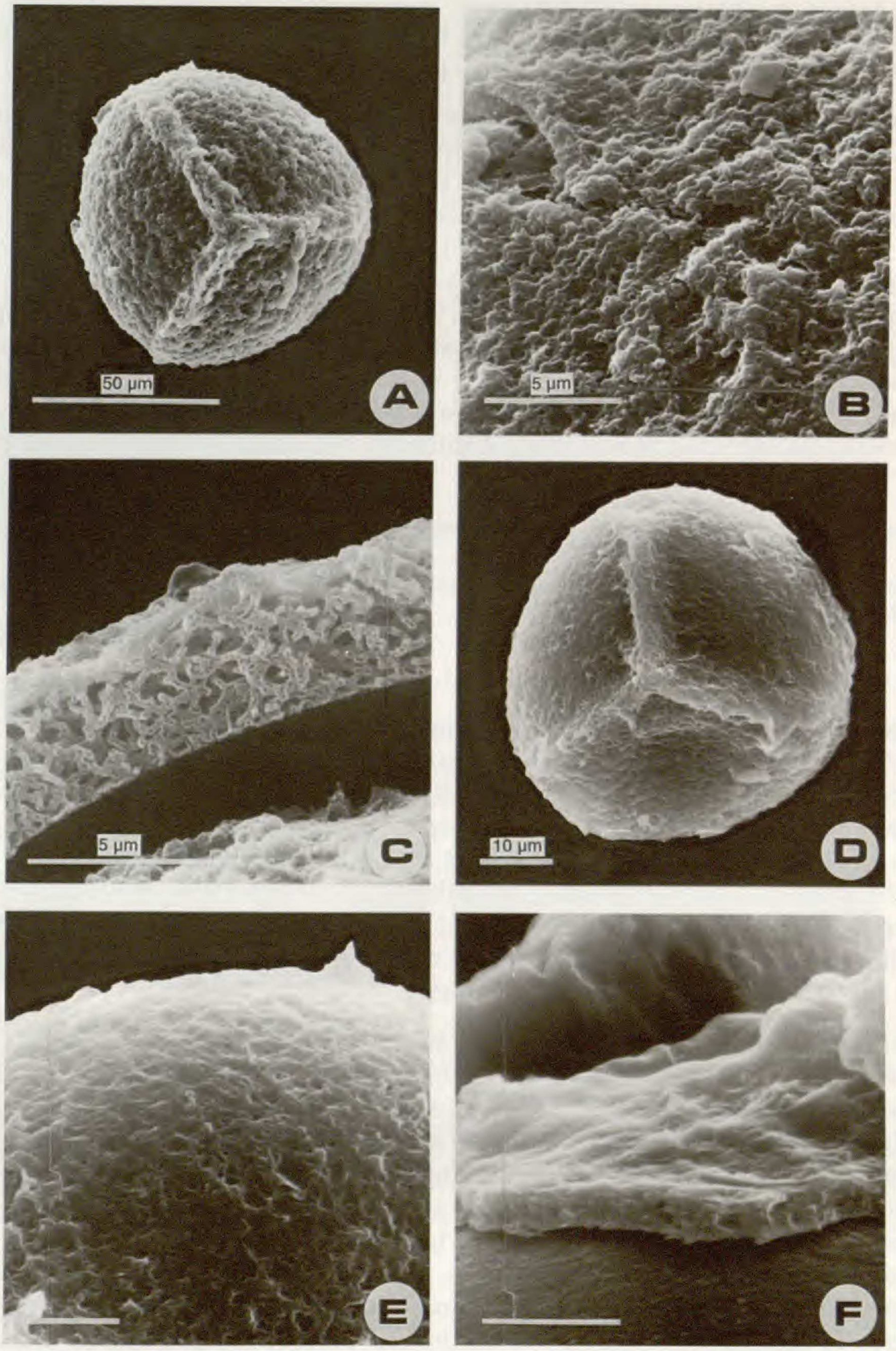

FIG. 2. A–C) *Cheilanthes bonariensis*. A) Proximal view. B) Surface detail, showing the rugulate perispore. C) Fractured perispore section, showing the thick middle complex layer with several levels of fused threads (*Sleumer & Vervoorst 2821*, LIL). D, E, F) *Cheilanthes* cf. *cucullans*. D) Proximal view. E) Surface detail, showing the rugulate perispore. F) Fractured perispore section, showing the thin perispore with a narrow middle layer (*Palací 34*, LP).

rugulate. Rugae low 0.25–0.5 (0.4) μm high, densely packed, placed in a concentric pattern. Background sculpture: granulate.

COMMENTS.—The number of spores per sporangium was both 32 and 16 in all the specimens studied. These data support earlier observations that *C. bonariensis* is a triploid, apomictic species (Knobloch et al., 1973). Well-developed trilete spores (70–80 μm De), were found in *Sleumer and Vervoorst 2821* (LIL), but few monolete spores (115.2 μm DE), were noted as well. In *C. bonariensis,* as in other low-ornamented spores, the perispore covers and modifies the laesura, making it more evident and thick when seen in surface view. Some specimens showed the perispore cracked after acetolysis. There is no agreement between the features of the spores in our samples and the ones studied by Naab (1987). In our study, the perispore was strongly attached to the exospore. However our samples show strong similarities to materials from Bolivia studied by Tryon and Lugardon (1991).

SPECIMENS STUDIED.—Jujuy, Humahuaca, *West 6309* (LIL); Salta, Caldera, Potrero del Castillo, *Sleumer & Vervoorst 2821* (LIL 395520); Catamarca, Andalgalá, *Sleumer 1846* (LIL); Tucumán, Tafí, Siambón, *Lillo 1040* (LIL); Chicligasta, de El Bolsón a la Cascada, *Meyer 18188* (LIL); Amaicha, El Molle, unknown coll. s.n. (LIL 16924).

4. **Cheilanthes buchtienii** (Rosenst.) R. M. Tryon.—Fig. 3A–D.

DESCRIPTION.—Spores: trilete, with triangular outline in polar view. De (a) 56.7–61.2 (58) μm, De (b) 60.3–68.4 (63) μm, Dp 47.7–52.2 (49.9) μm. Laesura arms: 22.5–27.0 (24.7) μm long, 3.6 μm high, reaching the equator, tenuimarginate or indistinctly marginate. Exospore: yellow, 1.3–2.0 (1.6) μm thick, 2-layered, smooth. Perispore: brown, 1.8–3.6 (2.5) μm thick, closely attached to the exospore, 3-layered; inner layer thin; middle layer well developed, composed of fused threads in several levels; outer layer thin; closed structure (Morbelli and Michelena, 1989); cristate to cristate-reticulate. Cristae 1.7–2.7 (1.9) μm high. Background sculpture: perforate.

COMMENTS.—The specimen *Barkley 19AR 649* (LIL) contained 64-, 32- and 16-spored sporangia, with evident differences in spore-sizes. However, there was no significative variation in spore-sizes in *Cuezzo and Legname 2257* (LIL), which nevertheless has 64- and 32-spored sporangium. Different specimens show cristate patterns of varying height. In this case, as in cristate-reticulate spores, the perispore covers and modifies the laesura, making it unclear or indistinguishable when seen in surface. Sometimes the perispore is cracked and detached after acetolysis. There are spores with different wall color, perispore thickness, and complexity, which might reflect differences in degree of maturation. Contrary to Michelena (1989), big differences were not found between the spores of *C. buchtienii* and its variety *ventanensis* (Weath.) Capurro. Contrary to Naab (1987), we found that the perispore was strongly attached to the exospore.

SPECIMENS EXAMINED.—Salta, Santa Victoria, Santa Victoria, *Meyer 4830* (LIL); Tucumán, Trancas, Las Burras, Río Las Burras, *Cuezzo & Legname 2257* (LIL); Catamarca, Ambato, El Rodeo, *Barkley*

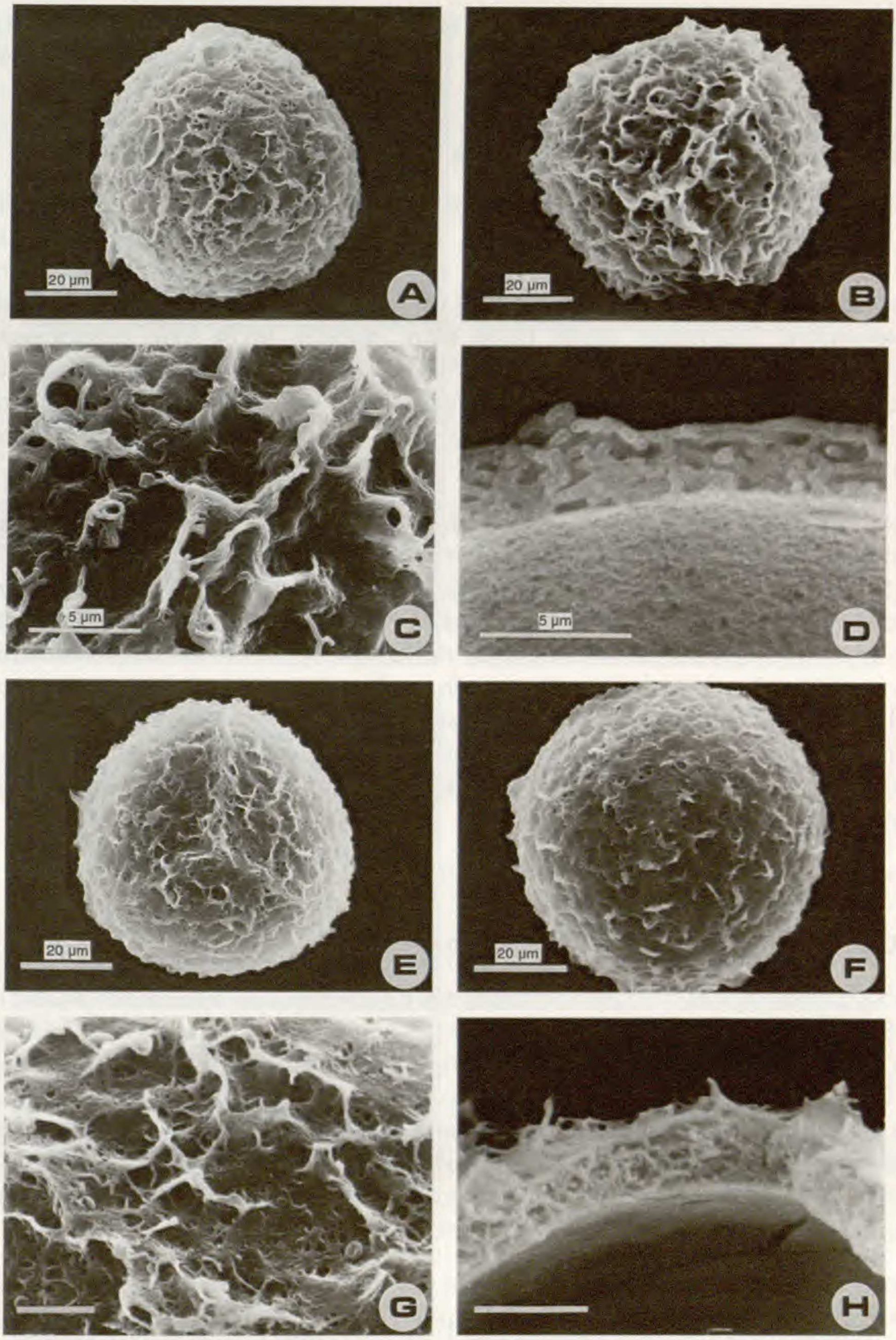

FIG. 3. A–D) *Cheilanthes buchtienii.* A) Distal view. B) Proximal view. C) Surface detail, showing a cristate to cristate-reticulate perispore. D) Fractured perispore section, showing the thick middle layer with several levels of fused threads (*Meyer 4830*, LIL). E-H) *Cheilanthes volcanensis.* E) Proximal view. F) Distal view. G) Surface detail, showing the cristate sculpture of the perispore. H) Fractured perispore section, showing the complex middle layer with several planes of thread junctions (*Lillo 3460*, LIL).

19AR 649 (LIL); Santiago del Estero, Guasayán, Tazana, *Pierotti* s.n. (LIL 109887); La Rioja, Quebrada de Los Noques, Malanzán, *Vera de Gandio* s.n. (LIL); San Luis, Junín, Piedra Blanca, *Digilio & Grassi 2178* (LIL).

5. **Cheilanthes cf. cucullans** Fée.—Fig. 2D–F.

DESCRIPTION.—Spores: trilete with triangular outline in polar view. De 46.2–52.5 (50.4) μm. Laesura arms: straigth, 25–26.3 (25.6) μm long, 2.5 μm high, tenuimarginate, reaching the equator. Exospore: not seen with ligth microscope, smooth in SEM view. Perispore: 0.7–1.2 μm thick, strongly attached to the exospore, 3-layered; inner layer thin; middle layer low, composed of threads fused in few levels; outer layer thin; closed structure (Morbelli and Michelena, 1989); rugulate. Rugulae low, 0.2–0.5 μm high. Background sculpture: echinulate-punctate. Some spores with scarcely differentiated threads plus echinula.

COMMENTS.—The presence of *C. cucullans* in Argentina is somewhat unusual because this species is otherwise restricted to Mexico and Guatemala. The specimen studied appears morphologically identical to those of North and Central America. The species was cited as present in South America by de la Sota and Ponce (1992). The outer layer of the perispore is so thin that it scarcely covers the structure below. Spores from the scant material were not examined with LM, thus exospore thickness and exospore/perispore color could not be estimated. It is necessary to point out the similarity between the spores of *C. cf. cucullans* and the closely related *C. notholaenoides*, the latter studied by Morbelli and Michelena (1989).

SPECIMENS EXAMINED.—Salta, La Viña, *Palací 34* (LP).

6. **Cheilanthes obducta** Mett. ex Kuhn.—Fig. 4A–D.

DESCRIPTION.—Spores: trilete, with triangular to triqueter outline in polar view. De: 56.7–61.2 (58.4) μm; Dp: 58.5–66.6 (63.1) μm. Laesura arms: straight, 20.7 36.0 (25.0) μm long, 3.6–6.3 (5.1) μm high, tenuimarginate, reaching the equator. Exospore: yellow to brown, 1.35 μm thick, 2-layered, smooth. Perispore: pale yellow, 0.2–0.6 μm thick, 3-layered; inner layer thin; middle layer low; outer layer thin; closed structure (Morbelli and Michelena, 1989); echinate-baculate. Echina/baculae 0.9–1.8 (1,3) μm high with forked bases. Background sculpture: granular. Granules sometimes grouped.

COMMENTS.—The description was based on *de la Sota 1241*, in which the presence of echinae or baculae on the perispore surface was not a constant feature. Spores in *Türpe et al. 4634* are larger than in the others samples. They are De 59.4–66.7 (63.2) μm; Dp 67.5–82.8 (72.9) μm, and the sporoderm is thicker as well; this may reflect a ploidy difference. The same material has abnormalities, such as double and aborted spores. It also contains 32-spored sporangia, which indicates that is probably apomictic. Three types of perispore sculpture have been recognized in different specimens: granular (*Morello and Cuezzo*

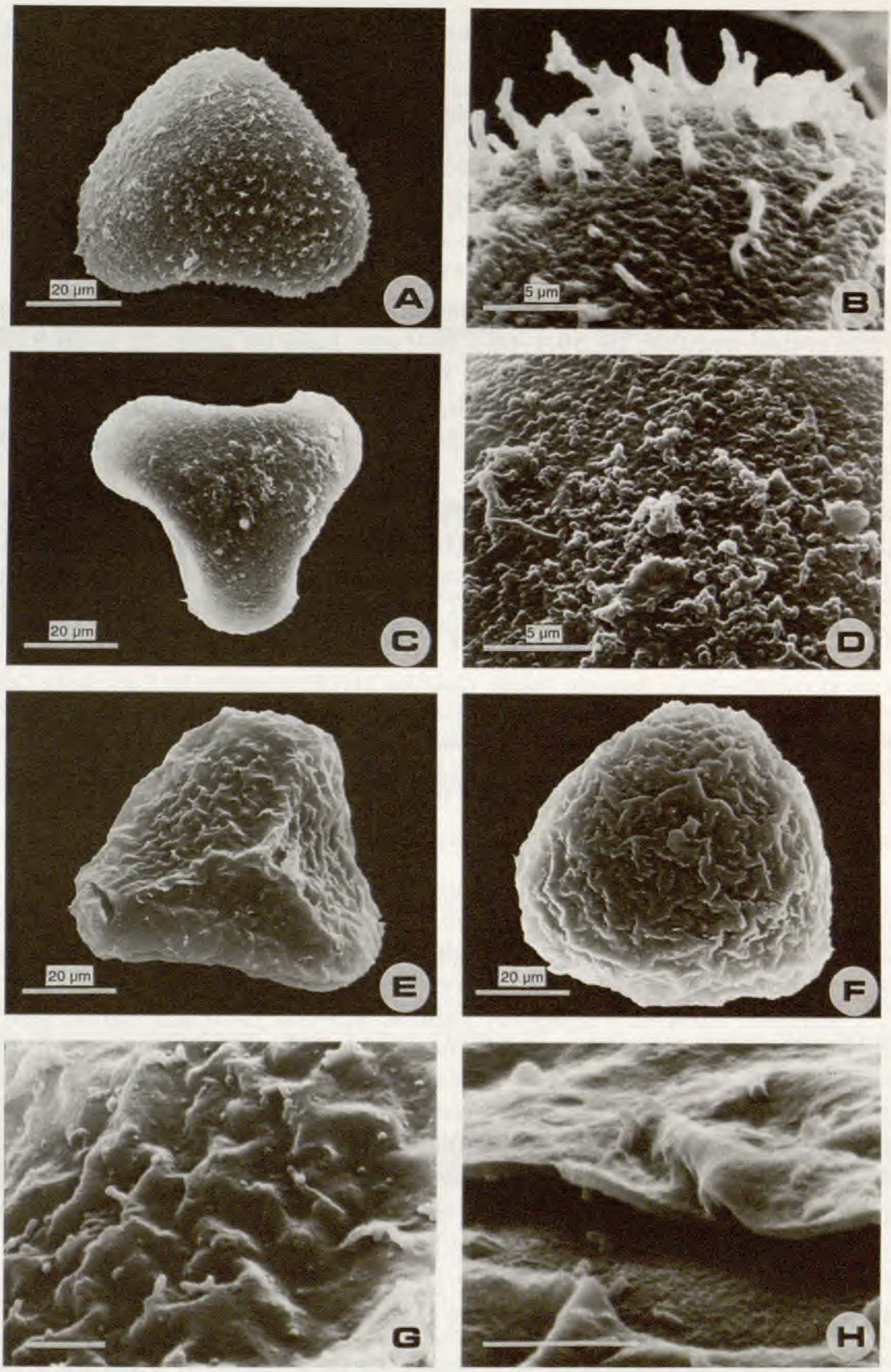

FIG. 4. A–D) *Cheilanthes obducta*. A) Distal view. B) Surface detail, showing the granulate-baculate perispore (*de la Sota 1241*, LIL). C) distal view. D) Surface detail, showing a granulate perispore (*Morello & Cuezzo* s.n., LIL 505245). E–H) *Astrolepis sinuata*. E) Proximal view, showing the folded perispore. F) distal view. G) Surface detail, showing short folds of the perispore. H) Fractured perispore section, showing the thin perispore, and the folds and granulate sculpture of the exospore beneath (*Lillo 3860bis*, LIL).

s.n., LIL 505245), rugulate (*Castellanos* s/n, LIL 325315) and equinate-baculate (*Türpe et al. 4634,* LIL).

SPECIMENS EXAMINED.—Jujuy, Santa Bárbara, Laguna La Brea, *Türpe et al. 4634* (LIL); Salta, San Martín, Aguaray, *de la Sota 1241* (LIL); Formosa, Bermejo, al N de Pozo de Maza, *Castellanos* s.n. (LIL 325315); Tucumán, Capital, Barranca Colorada, *Venturi 846* (LIL); Catamarca, Sierra del Alto, *Morello & Cuezzo* s.n. (LIL 505245); Ambato, Quebrada de Los Nacimientos, *Castillón* s.n. (LIL 17007); *La Rioja,* Sierra Alta, *Castellanos* s.n. (LIL 96052).

7. **Cheilanthes squamosa** Hook. & Grev.—Fig. 1D–F.

DESCRIPTION.—Spores: trilete, with triangular outline in polar view, convex sides and round angules; De 59.4–66.7 (63) μm. Laesura arms: 22.5–28.8 (26.4) μm long, straight, elevated. Exospore: 6.2–7.2 (6.4) μm thick, 2-layered, verrucate. Verrucae 5.5–6.3 (5.7) μm high, 7.2–10.8 (9.2) μm in diam., some of them fused. Perispore: pale yellow, 0.2–0.6 (0.5) μm thick, strongly attached to the exospore, 1-layered, scabrate.

COMMENTS.—There are variations in spore-sizes and apertural types in this group. In *Sleumer & Vervoorst 2849* (LIL), 32-spored sporangia were found. The spores have different sizes (two normal distributions in the same sample: 59–67 μm and 72–79 μm in equatorial diameter). Monolete (115.2 μm diam) and intermediate (72 μm diam.) spores also were found.

SPECIMENS EXAMINED.—Jujuy, Estación Volcán, *Castillón 24* (LIL), *Castillón 23* (LIL); Salta, Caldera, Potrero del Castillo, *Sleumer & Vervoorst 2849* (LIL); Tucumán, Chicligasta, Bassin Río Cochuna, *Halloy A-137* (LIL); Nevados del Aconquija, *Halloy* s.n. (LIL 559435); Catamarca, Belén, Quebrada del Río Blanco, *Sleumer & Vervoorst 2526* (LIL); Andalgalá, Cuesta de La Negrilla, *Sleumer 2703* (LIL); Andalgalá, Cerro Yutuyaco, *Sleumer 2737* (LIL); Capillitas, *O'Donell 1369* (LIL).

8. **Cheilanthes volcanensis** de la Sota.—Fig. 3E–H.

DESCRIPTION.—Spores: trilete with circular to subcircular outline in polar view; De 45.9–54.0 (50.8) μm; Dp 45–54.0 (50.4) μm. Laesura arms: 19.8–28.8 (23.2) μm long, 2.2–6.3 (3.7) μm high, straight, tenuimarginate or indistinctly marginate, reaching the equator. Exospore: yellow to brown, 1.5–5.2 (2.4) μm thick, 2-layered, smooth. Perispore: yellow, 2.5–3.1 (2.8) μm thick, strongly attached to the exospore, 3-layered; inner layer thin; middle layer well developed composed of threads fused in several levels; outer layer thin; closed structure (Morbelli and Michelena, 1989); cristate. Cristae short, 0.7–2.1 (1.3) μm high; margins supraornate, echinulate; concentrically placed in the distal face. Background sculpture: cristate-perforate.

COMMENTS.—The perispore is cracked and detached as a consequence of the chemical treatment. *Cheilanthes volcanensis* is closely related to *C. marginata.* Most sporophytic features, except the rhizome, are similar in these species, but they can be differentiated easily by their spores.

SPECIMENS EXAMINED.—Tucumán, Chicligasta, Bassin Río Cochuna, *Halloy A-134* (LIL); Cumbre del Malamala, *Lillo 3460* (LIL); Tafí, Ciénaga, Cerro de Las Aguadas, *Lillo 1310* (LIL).

DISCUSSION

From analysis of Tables 2 and 3, which synthesize the data of the species of *Cheilanthes* and *Astrolepis* that grow in northwestern Argentina (Table 2

TABLE 2. Spore characteristics found in Argentinean species of cheilanthoid ferns correlated with species groups recognized by Tryon and Tryon (1982) and Ponce and Morbelli (1989). Data for species indicated with an asterisk (*) are from the first part of this study (Morbelli & Michelena, 1989). Species in parentheses were not studied in this paper (data from other sources).

Species groups and single species	Argentinian Species	Exospore sculpturing	Perispore sculpturing	Perispore structure
C. fraseri	*C. bonariensis*	smooth	rugulate	3-layered
	C. buchtienii		cristate	
	(*C. hypoleuca*)		cristate-reticulate	
C. marginata	*C. marginata**	smooth	rugulate	3-layered
	C. volcanensis		ridged	
	*C. poeppigiana**		cristate	
	(*C. hieronymi*)			
C. microphylla	*C.* cf. *cucullans*	smooth	rugulate	3-layered
	*C. notholaenoides**			
C. micropteris	*C. micropteris**	smooth	cristate	3-layered
	*C. pilosa**		cristate-reticulate	
	*C. pruinata**			
C. myriophylla	*C. myriophylla**	smooth	rugulate	3-layered
C. dichotoma	(*C. dichotoma*)	smooth	cristate	3-layered
	(*C. orbignyana*)		cristate-reticulate	
	(*C. sarmientoi*)			
	(*C. tweediana*)			
C. glauca	(*C. glauca*)	smooth	cristate-reticulate	3-layered
C. obducta	*C. obducta*	smooth	echinate	3-layered
			baculate	
C. squamosa	*C. arequipensis*	verrucate	scabrate	1-layered
	C. squamosa			
A. sinuata	*A. sinuata*	rugulate	folded	1-layered

includes all Argentinean species), the following comments can be made. Seven types of sculpture have been found (Table 2). They are: verrucate, rugulate, equinate-baculate, ridged, cristate, cristate-reticulate, and folded. Three of these types, equinate-baculate, verrucate, and folded, were not cited in the previous study by Morbelli and Michelena (1989). The most frequent types were: rugulate (*C. myriophylla, C. notholaenoides, C. poeppigiana, C. bonariensis, C.* cf. *cucullans*), cristate (*C. micropteris, C. buchtienii, C. volcanensis*), and cristate-reticulate (*C. pilosa, C. pruinata, C. buchtienii*).

Three patterns of sporoderm structure were recognized. 1) Exospore strongly sculptured, verrucate; perispore 0.4–0.8 μm thick, 1-layered, finely sculptured; present in *C. arequipensis* and *C. squamosa*. (Tables 2, 3; Fig. 1).2) Exospore finely sculptured, rugulate; perispore 0.7–1.3 μm thick, 1-layered, folded, finely sculptured; present in *Astrolepis sinuata*. (Tables 2, 3; Fig. 4 E–H). Folds are present only in *Astrolepis*. The perispore is detached from the exospore only in places where the folds rise. Folded perispore differs from rugulate perispore in that the rugae are more compact. 3) Exospore smooth; perispore 2.0–4.5 μm thick, 3-layered, sculptured; inner layer thin, compact, attached to

TABLE 3. Comparative table of some spore features in *Cheilanthes* and *Astrolepis* species of northwestern Argentina. All measurements in μm. Exospore thickness is listed as mean values. Perispore thickness is listed as minimum and maximum values. For all measurements, elements of the sculpturing are excluded. Spores of *C.* cf. *cucullans* were not studied with light microscopy, thus details such as exospore thickness and perispore color were not seen.

Species	Equatorial diameter	Sporoderm pattern	Exospore thickness	Perispore thickness	Perispore color
A. sinuata	53–98	II	2.5	0.7–1.3	Pale brown to yellow
C. arequipensis	49–57	I	2.5	0.4–0.8	Hyaline
C. squamosa	59–67	I	6.4	0.2–0.6	Pale yellow
C. bonariensis	70–80	III	2.2	1.8–4.5	Pale yellow to yellow
C. buchtienii	57–61	III	1.6	1.8–3.6	Brown
C. cf. *cucullans*	46.0–52.5	III	—	0.7–1.2	—
C. obducta	57–61	III	1.3	0.2–0.6	Pale yellow
C. volcanensis	46–54	III	2.4	2.5–3.1	Yellow to brown

the exospore; middle layer composed of fused threads in one to several levels; outer layer thin and sculptured; present in most species of *Cheilanthes*. (Tables 2, 3). In *C.* cf. *cucullans* (0.7–1.2 μm thick) and *C. obducta* (0.2–0.6 μm thick), with a very thin perispore, 3 layers are still clearly distinguishable with LM. The 3-layered perispore of *Cheilanthes*, in spite of its complexity, is weak. It usually is broken into plates, even before any chemical treatment.

According to our observations and those in the literature (Tryon and Tryon, 1982), most cheilanthoids can be grouped by their vegetative features. These groups do not always fit with the associations based on palynological characters. However, spore morphology allows differentiation of closely related species within certain groups with homogenous sporophyte morphology. Such cases include the *C. marginata* group, in which *C. marginata* has ridged spores, *C. poeppigiana* has rugulate spores, and *C. volcanensis* cristate spores. Within the *C. fraseri* group, *C. bonariensis* has rugulate spores and *C. buchtienii* has cristate-reticulate ones, although they are apparently related, according to indument type. This last complex, in which a large number of species are from southern South America, should be revised, because its members present different types of rhizomes, lamina outlines, petiole cross-sections, pinnule margin modifications, and several types of spores. These suggest that the group may be polyphyletic.

In contrast, in other groups of closely related taxa studied previously, such as *C. micropteris* Sw. (Morbelli and Michelena, 1989) and *C. dichotoma* Sw. (Ponce and Morbelli, 1989) all members have cristate-reticulate spores. Minor variations can be documented in perispore thickness and sculpture among these species, such as lumina width and crista height, fusion, and margin characters (smooth or supraornate).

The spores of *C. obducta* are unique. The perispore sculpture is baculate-echinate, with a granulate background and a 3-layered structure. This morphologically isolated species also has other unique sporophytic features, such

as complex hairs composed of several cell types with tongue-and-groove fitting walls, bicellular glandular hairs, vein tips with a T or L form without enlarged tips, and dixylic vascular strands. The two bundles of xylem join at the laminar level. This type of xylem also is found with less frequency in *C. squamosa*. The dixylic structure had been mentioned for *Cheilanthes* by Ogura (1972).

Astrolepis sinuata, C. bonariensis, C. buchtienii, and *C. squamosa* show differences in spore number and size within a sample in most specimens, and in *C. obducta,* between samples. The differences in size are always associated with variations in color and laesura type. Monolete spores often are present in some specimens of *A. sinuata, C. bonariensis,* and in the species that belong to the "verrucate group" (*C. arequipensis* and *C. squamosa*). The reproductive behavior of these taxa should be studied in detail, as there are interesting connections among the spore numbers and types and apogamy, hybridization, ploidy levels, and xerophytism in *Cheilanthes* (Knobloch, 1969; Vida et al. 1971). Further cytological studies of Argentinean cheilanthoid ferns would be very informative.

CONCLUSIONS

The variation in spore morphology of *Cheilanthes* in the studied area is similar to those of other parts of the Americas (cf. Devi et al., 1971; Knobloch, 1969; Knobloch et al., 1970; Tryon and Tryon, 1973), with the exception of *C. obducta,* which does not have similarities with any other American, European, or African species. It has remarkable similarity with those of Australia, particularly to spores of *C. caudata* R. Br., which is endemic to Australia (cf. Chambers and Farrant, 1991; Tryon & Lugardon, 1991, Quirk et al., 1983).

Most *Cheilanthes* species of northwestern Argentina show sporoderm structural pattern III (see Discussion), with a 3-layered perispore. Nevertheless, according to our results (Morbelli et al., 1994) and those reported in the literature (Tryon and Lugardon, 1991), other cheilanthoid ferns, such as some species of *Argyrochosma, Notholaena, Pellaea,* and *Doryopteris,* have a similar structural pattern to *Cheilanthes.*

In spite of the relatively small geographic area studied, we suggest that spore morphology supports some of the taxonomic groups recognized by Tryon and Tryon (1982), such as that of *C. micropteris* and *C. dichotoma,* proposed by Ponce and Morbelli (1989); but not all, such as the *C. marginata* and *C. fraseri* groups. (see Discussion and Table 2).

The "verrucate complex" present in the study area, *C. arequipensis* and *C. squamosa* (with verrucate exospore and 1-layered perispore), is unique not only because of its sporoderm pattern, but because the species have only scales as lamina vestiture (i.e., no hairs) (Tryon and Tryon, 1973, 1982; Tryon and Lugardon, 1991). Other genera of Pteridaceae, such as *Cryptogramma* and *Hemionitis,* have a sporoderm pattern similar to that of the Andean "verrucate complex" (Tryon and Lugardon, 1991). We agree with previous authors that this complex might constitute a distinct genus. A systematic revision of this group is necessary.

Astrolepis sinuata, C. bonariensis, C. obducta, and *C. squamosa* are characterized by 32- and 16-spored sporangia. In *C. buchtienii,* we noted 64-, 32- and 16-spored sporangia. This variation in spore number may reflect an apogamous life cycle in these taxa. In most of these species, there also are different spore sizes and shapes within a sample, probably because of failures in premeiotic mitosis and sporogenesis processes within the sporangia.

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